

Regional Scale Climate Forcing of Mesozooplankton Dynamics in Chesapeake Bay

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ABSTRACT: A 16-yr (1985–2000) time series of calanoid copepod (*Acartia tonsa* and *Eurytemora affinis*) abundance in the upper Chesapeake Bay was examined for links to winter weather variability. A synthesis of sea level pressure data revealed ten dominant, winter weather patterns. Weather patterns differed in frequency of occurrence as well as associated precipitation and temperature. The two dominant copepod species responded differently to winter weather variability. *A. tonsa* abundance showed little response to winter weather and did not vary in abundance during wet or dry springs. *E. affinis* responded strongly to winter weather patterns that produced springs with high freshwater discharge and low salinities. During wet springs, *E. affinis* abundance increased overall and its area of dominance extended further down estuary. The different response of the two species is likely related to several factors including residence time, development time, salinity tolerance, food limitation, and life history strategy. Important fish species that rely on zooplankton as food resources were also related to winter weather variability and spring zooplankton abundance. *Morone saxatilis* (striped bass) and *Anchoa mitchilli* (bay anchovy) juvenile indices were positively and negatively correlated to *E. affinis* abundance, respectively.

Introduction

The distribution and abundance of marine organisms are influenced by a variety of abiotic and biotic factors that are directly related to climate (Cushing and Dickson 1976). While this is not a novel insight, climate research has recently gained importance as investigators focus on detecting the biological response of systems to human-induced climate change (Walther et al. 2002; Parmesan and Yohe 2003). This research has often involved the use of localized studies designed to detect a global phenomenon through the use of indicator species, changes in species phenology, shifts in ranges of species (including species invasions), and links to environmental variables or climate indices (Walther et al. 2002). The linkages between environmental and biological variables and climate indices have been thoroughly explored, e.g., El Niño-Southern Oscillation in the equatorial Pacific Ocean (Pearcy and Schoener 1987; Sugimoto et al. 2001) and the Pacific Decadal Oscillation in the north Pacific Ocean (Hollowed et al. 2001; Royer et al. 2001). Detection of climate effects on Europe and the eastern United States has often used the North Atlantic Oscillation (NAO), a climate index that measures the difference in sea level pressure between Iceland and the Azores (Hurrell 1995; Ottersen et al. 2001; Parsons and Lear 2001). The NAO has been shown to influence multiple trophic

levels (Ottersen et al. 2001), alter copepod species composition and abundance (Fromentin and Planque 1996; Planque and Reid 1998; Planque and Taylor 1998), and alter fish assemblages in the north Atlantic Ocean (Attrill and Power 2002).

Chesapeake Bay has also been the focus of climate and ecosystem response research (Cronin et al. 2000; Gibson and Najjar 2000; Wood 2000; Austin 2002). Austin (2002) described low frequency patterns of climate variability that resulted in dramatic regime shifts in Bay species. These regime shifts affect the recruitment of several commercially important species such as *Morone saxatilis* (striped bass), *Brevoortia tyrannus* (menhaden), *Crassostrea virginica* (Eastern oyster), and *Callinectes sapidus* (blue crab; Austin 2002). The dominant regimes of weather from 1960 onward were a cold-dry period (1960s) and two warm-wet periods (1970s, 1990s; Austin 2002). Wood (2000) also described climate forcing of anadromous and coastal and shelf spawning fish species using synoptic climatology. These types of warm-cool or wet-dry cycles seem to be repeated throughout the climatological record. Evidence from sediments suggest that Chesapeake Bay experienced a series of wet-dry cycles over the past 500 yr (Cronin et al. 2000). During these wet-dry periods, the salinity in the mesohaline portion of Chesapeake Bay may have changed as much as 10–15 (Cronin et al. 2000). Gibson and Najjar (2000) modeled the potential effect of human-induced climate change on Chesapeake Bay stream-flow and salinity and found that salinity may drop by as much as 27% in the upper Bay.

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Despite the usefulness of climate indices in Europe and the north Atlantic, the NAO has not been strongly linked to climate or weather variability in the mid-Atlantic region (Read 2002; Stenseth et al. 2003; Miller et al. 2006). In order to classify climate in the mid-Atlantic region, we used a synoptic climatology approach (Yarnal 1993). Synoptic climatology classifies weather variability on smaller spatial (1,000–2,500 km) and temporal scales (interannual) using a series of statistical techniques. The procedure is designed to detect similar modes of variance in sea level pressure (SLP) data over a predefined region (Yarnal 1993; Miller et al. 2006). The result is a small set of SLP maps that represent the common weather patterns experienced in the predefined region. The frequency of occurrence of the patterns and their relationship to surface variables, i.e., down-scaling, can then be used to describe the weather experienced by a region during a time period of interest (Miller et al. 2006).

We focused our study on the connection between winter climate patterns and spring conditions in Chesapeake Bay. The major driver of biological variability in the upper Bay during spring is freshwater input (Harding 1994; Kimmel and Roman 2004). The Susquehanna River contributes >50% of the total freshwater input into Chesapeake Bay (Schubel and Pritchard 1986). Winter climate patterns are strongly correlated to spring freshwater input into Chesapeake Bay (Miller et al. 2006). Precipitation, in the form of snow, is stored in the Susquehanna River watershed during winter (December, January, and February) and is delivered to the Bay in the spring (March, April, and May), with peak input typically occurring in late March (Najjar 1999). Kimmel and Roman (2004) have shown that freshwater flow can affect mesozooplankton abundance and community composition in Chesapeake Bay. Our goal in this study was to examine the links between climate and mesozooplankton dynamics in Chesapeake Bay, particularly during wet-dry cycles. We investigated the influence of winter weather variability on estuarine conditions in the spring. We report on how wet-dry winters affect physical conditions, residence time, zooplankton abundance, and development time, as well as the juvenile indices of two important fish species that use zooplankton as a primary food source for their larvae (*M. saxatilis* [striped bass]) or adults (*Anchoa mitchilli* [bay anchovy]).

Materials and Methods

WEATHER PATTERN DATA

Methods for classifying SLP data into weather patterns are presented in Miller et al. (2006), but

a brief summation is presented here. We used an eigenvector based classification method to generate the synoptic weather types based on methods described in Yarnal (1993). We used SLP (mb) data acquired from the National Center for Atmospheric Research (<http://www.ncar.ucar.edu>) in an area bounded by 25–50°N and 65–100°W (Miller et al. 2006) to define our weather pattern types. Once identified, each weather pattern was downscaled, i.e., related to surface weather data. The surface weather data consisted of monthly mean air temperature and precipitation for the Susquehanna River watershed and was compiled from 8 climate regions, spanning 3 states (New York: 1, 2; Pennsylvania: 4, 5, 6, 7, 8; and Maryland: 6). The regional climate data was acquired from the National Climate Data Center (NCDC; <http://cdo.ncdc.noaa.gov>). Temperature and precipitation values were weighted by area to produce a single estimate for the entire basin (Miller et al. 2006). We also used the NCDC Climate at a Glance (www.ncdc.noaa.gov/oa/climate/research/cag3/cag3.html) data to define the average conditions in the northeastern U.S. during two wet (1994 and 1998) and two dry years (1985 and 1995).

Weather pattern anomalies were calculated for the winter (December, January, and February) of each year, e.g., the winter of 1984 represents December of 1983 and January and February of 1984. For each weather pattern and each year, we calculated:

$$d_{\text{win}} = \sum_{i=\text{Dec}}^{\text{Feb}} d_i$$

where d_{win} is the number of days that each weather pattern occurred during the winter of each year (1951–2000), and d_i is the number of days each weather pattern occurred in a month. Next, we computed

$$d_{\text{LTM}} = \frac{1}{n} \sum d_{\text{win}}$$

where d_{LTM} is the long-term arithmetic mean number of days each weather pattern occurs in the winter for the period 1951–2000, and n is the number of years in the data record (1951–2000). The anomaly was calculated using the formula:

$$A_{\text{wp}} = d_{\text{win}} - d_{\text{LTM}}$$

where A_{wp} is the weather pattern anomaly in number of days, and d_{win} and d_{LTM} are as above.

PHYSICAL DATA

Susquehanna River discharge data was acquired from the U.S. Geological Survey gauging station at

Harrisburg, Pennsylvania (<http://waterdata.usgs.gov>). We chose to use the Harrisburg gauging station because of the long data record, from 1890 to the present. A gauging station more proximate to Chesapeake Bay exists at the Conowingo Dam, Maryland, but the data record only extends back to 1967. Flow is linearly related ($r^2 = 0.99$) between the Harrisburg and Conowingo gauging stations (Miller et al. 2006). Daily discharge values were reported in $\text{m}^3 \text{s}^{-1}$ and were converted to m^3 using the formula:

$$Q_d = Q \times s$$

where Q_d is the amount of discharge (m^3), Q is the average daily discharge rate ($\text{m}^3 \text{s}^{-1}$), and s is the number seconds per day. We also computed spring cumulative discharge. We calculated:

$$Q_{\text{spr}} = \sum_{i=\text{Mar}}^{\text{May}} Q_d$$

where Q_{spr} is the cumulative discharge for spring of each year (1951–2000). Next, we computed:

$$Q_{\text{LTM}} = \frac{1}{n} \sum Q_{\text{spr}}$$

where Q_{LTM} is the long-term arithmetic mean, spring discharge for the period 1951–2000. The anomaly was calculated using the formula:

$$A_Q = Q_{\text{spr}} - Q_{\text{LTM}}$$

where A_Q is the discharge anomaly.

Salinity and water temperature ($^{\circ}\text{C}$) data were acquired from the U.S. Environmental Protection Agency's Chesapeake Bay Program (CBP) website (<http://www.chesapeakebay.net>) for station CB3.3C for the period 1985–2000. We chose station CB3.3C as a reference point for the upper Chesapeake Bay since it lies approximately equidistant from the Susquehanna River mouth and the mouth of the other major source of freshwater input into the Bay, the Potomac River. Station CB3.3C is in the transition zone between oligohaline (0–5 salinity) and mesohaline (5–15) salinity regions. Arithmetic mean, depth integrated (see Kimmel and Roman 2004), monthly salinity or water temperature values (X_m) were used to compute a spring arithmetic mean using the formula:

$$X_{\text{spr}} = \frac{1}{3} \sum_{i=\text{Mar}}^{\text{May}} X_m$$

where X_{spr} is the arithmetic, monthly mean salinity or water temperature for spring (March, April, and

May) of each year (1951–2000). Next, we computed

$$X_{\text{LTM}} = \frac{1}{n} \sum X_{\text{spr}}$$

where X_{LTM} is the long-term arithmetic mean, spring salinity or water temperature, and n is the number of years in the period 1951–2000. The anomaly was calculated using the formula:

$$A_X = X_{\text{spr}} - X_{\text{LTM}}$$

where A_X is the salinity or water temperature anomaly. We also computed arithmetic mean, winter water temperatures and salinities for use in regression models. These values were arithmetic mean, depth integrated water temperatures ($^{\circ}\text{C}$) or salinities for the winter (December, January, and February) for each year (1985–2000; see Kimmel and Roman 2004).

We calculated residence time using the freshwater fraction method (Dyer 1997), which was considered an estimate of the residence time during spring. Freshwater fraction f is determined by:

$$f = \frac{s_0 - S}{s_0}$$

where S is the average salinity of the estuary (we considered this to be the upper Chesapeake Bay, greater than 38.75°N) and s_0 is the salinity of the adjacent water body with which the estuary communicates (we considered this to be the middle bay, an area bounded by 38.75°N and 37.92°N). Residence time, T , is related to freshwater fraction by:

$$T = f \frac{V}{R}$$

where V is the volume of the estuary (for the upper Bay, $8.60 \times 10^9 \text{ m}^3$; Jung and Houde 2003) and R is the freshwater inflow (for April). The upper Chesapeake Bay communicated with the strongly stratified main stem of the Chesapeake Bay estuary. We used mean, depth integrated, April salinity values for this region and for each year to represent S for the upper Bay.

BIOLOGICAL DATA

Mesozooplankton abundance (number m^{-3}) data were acquired from the CBP monitoring program. Mesozooplankton abundance was used for stations CB2.2, CB3.3C, CB4.3C and CB5.2. A detailed description of the mesozooplankton data set can be found at <http://chesapeakebay.net/> (CBP 2000) and in Kimmel and Roman (2004). Arithmetic mean, monthly (see Kimmel and Roman 2004) *Acartia tonsa* or *Eurytemora affinis* abundance (number m^{-3}) values (Y_m) were used to compute a spring,

average abundance for the months March, April, and May using the formula:

$$Y_{\text{spr}} = \frac{1}{3} \sum_{i=\text{Mar}}^{\text{May}} Y_m$$

where Y_{spr} is the spring average abundance for either *A. tonsa* or *E. affinis*.

M. saxatilis and *A. mitchilli* juvenile index data were acquired from the Maryland Department of Natural Resources (<http://www.dnr.state.md.us/fisheries/juvinindex/>). Juvenile index surveys are conducted three times a year at 22 locations in the Maryland portion of Chesapeake Bay. The survey has been conducted since 1954. Fish are collected using a 30.5×1.24 m bagless beach seine and collected fish are separated into 0 and 1+ age groups. Geometric mean, annual juvenile index values (Z) are calculated for each species and a higher juvenile index value indicates a stronger year class. The survey is designed to assess the annual variation and long-term trends in the relative abundance of over 100 species of young-of-the-year fish. For each species, we computed

$$Z_{\text{LTM}} = \frac{1}{n} \sum Z$$

where Z_{LTM} is the long-term arithmetic mean for the period 1957–2000 (*M. saxatilis*) and 1959–2000 (*A. mitchilli*), and n is the number of years in the data record. The anomaly for each year was calculated using the formula:

$$A_Z = Z - Z_{\text{LTM}}$$

where A_Z is the *M. saxatilis* or *A. mitchilli* geometric, mean anomaly.

STATISTICAL ANALYSES

Mesozooplankton data were related to weather patterns in multiple ways. *A. tonsa* or *E. affinis* spring abundance (number m^{-3}) was used as a dependent variable in a stepwise regression model. The independent variables were the winter frequency of each weather pattern (days), winter water temperature ($^{\circ}\text{C}$), and winter salinity. We selected winter salinity and winter water temperature as possible predictors because they integrate effects of weather prior to the previous winter. We chose stepwise regression in order to reduce the number of nonsignificant variables in the model. Only variables significant at the $\alpha = 0.10$ level were retained in the model. We also calculated the adjusted r^2 value (r_{adj}^2) for each model to account for the effect of a potentially large number of predictor variables.

TABLE 1. Winter (December, January, and February 1985–2000) weather pattern frequency of occurrence (d), percent (%) of total occurrence, mean daily surface air temperature, and precipitation associated with each weather pattern.

Weather Pattern	Days of Occurrence	%	Mean (\pm SD) Winter Daily Temperature ($^{\circ}\text{C}$)	Mean (\pm SD) Daily Precipitation (mm)
1	105	7.3	0.47 (4.62)	3.21 (4.90)
2	236	16.4	-5.78 (5.24)	1.43 (3.20)
3	95	6.6	-3.40 (4.31)	3.03 (4.89)
4	65	4.5	-0.71 (4.61)	4.98 (6.97)
5	234	16.3	-0.21 (5.02)	2.49 (4.24)
6	101	7.0	-2.98 (4.90)	1.91 (3.88)
7	201	14.0	-4.62 (4.80)	2.23 (4.11)
8	51	3.5	0.32 (4.68)	3.80 (4.96)
9	128	8.9	-0.38 (5.25)	2.20 (3.85)
10	223	15.5	-3.75 (5.26)	1.43 (2.93)
n = 1,439			$\bar{x} = -2.104$ (2.26)	$\bar{x} = 2.67$ (1.11)

We computed r_{adj}^2 using the formula:

$$r_{\text{adj}}^2 = r^2 - \left[\frac{(k-1)}{(t-k)} \right] (1 - r^2)$$

where r^2 is the original model output, k is the number of individual variables, and t is the total number of observations. All statistical analyses were conducted using S-PLUS 6.0 (Insightful, Seattle, Washington) statistical analysis software.

In order to compare results from different winter climate periods we chose to designate two years as dry (1985 and 1995) and two years as wet (1993 and 1998). A brief comparison of the two years shows that 1985 and 1995 had below average freshwater input and 1994 and 1998 had above average freshwater input (see results below). We grouped these two wet and dry years because they were consistent in terms of discharge, salinity, and temperature (see below).

Results

WEATHER PATTERNS

A total of 10 weather patterns were identified. Weather patterns were typically characterized by dominant high or low pressure systems. Four weather patterns (2, 5, 7, and 10) accounted for 62.2% of the winter weather pattern frequency (Table 1). These weather patterns varied in their associated temperatures and precipitations and corresponded to distinct climate patterns that have been identified by other researchers (Davis et al. 1993, 1997). A full description of each weather pattern type may be found in Miller et al. (2006).

Weather pattern anomalies for two dry years (1985 and 1995) did not show many similarities (Fig. 1). The anomalies were often opposite in sign and showed no real pattern between the 2 yr. Three weather patterns did show the same anomaly sign between the two years: weather patterns 4, 7, and 10.

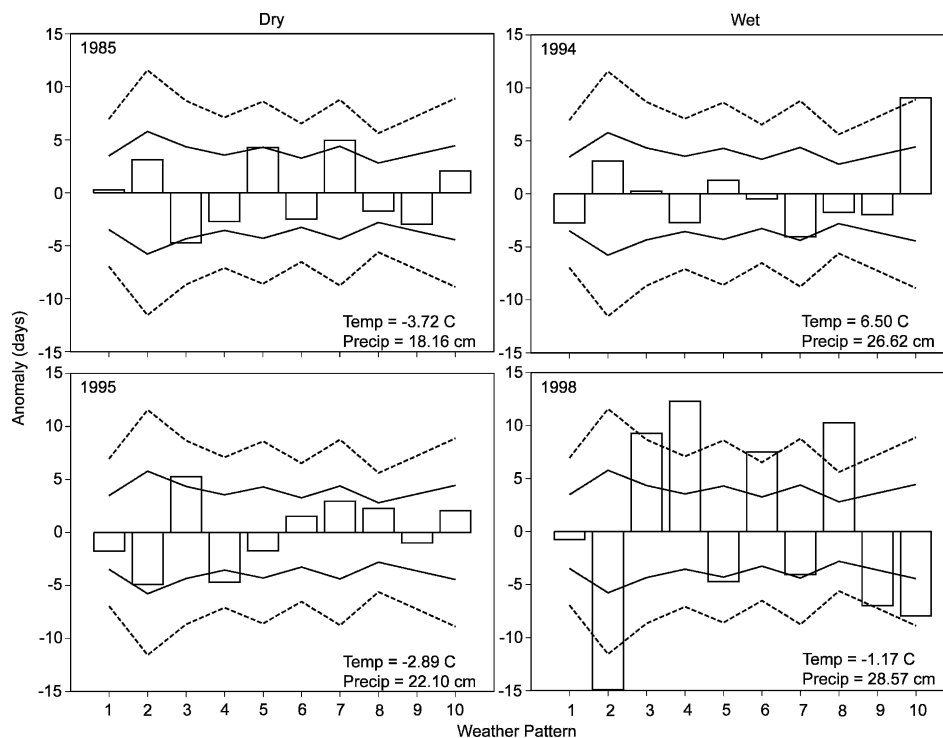


Fig. 1. Previous winter (December, January, and February) weather pattern anomalies for two dry (1985, 1995) and two wet (1994, 1998) springs (subsequent March, April, and May). Temperature (Temp) values are the winter mean temperature for the northeastern U.S. Precipitation (Precip) values are the cumulative winter precipitation for the northeastern U.S. (Climate at a Glance, National Climate Data Center). Solid line represents ± 1 and the dashed line represent ± 2 standard deviations from the mean (0).

Weather pattern 4 was negative in both years and this pattern is associated with high precipitation and is normally infrequent during the winter (Table 1). Weather patterns 7 and 10 had positive anomalies and are both associated with below average precipitation during winter. None of the weather patterns during the two dry years were considered extreme deviations, as no patterns exceeded two standard deviations from the long-term mean.

Weather pattern anomalies for the two wet years (1994 and 1998) also did not show a great deal of similarity (Fig. 1). Weather patterns 7 and 9 showed the same negative anomaly in both years and both patterns were associated with below average precipitation (Table 1). The wet year 1994 had a strong, positive anomaly of weather pattern 10, a deviation of >2 standard deviations from the long-term mean (Fig. 1). This was surprising because the pattern was associated with low precipitation (Table 1). The wet year 1998 had multiple patterns that deviated strongly from their long-term mean values (Fig. 1). Weather patterns 2, 9, and 10 showed large, negative deviations and weather patterns 3, 4, 6, and 8 showed strong positive deviations. Patterns 2, 6, and 9 were associated with low precipitation and patterns 3, 4, and 8 with above average precipitation (Table 1). The strong positive deviation of pattern 6

was surprising because it was associated with low precipitation. This pattern shared an association with cold temperatures, as did weather pattern 10 in 1994 (Fig. 1, Table 1).

PHYSICAL VARIABILITY

Spring, freshwater discharge from the Susquehanna River was below average during 1985–1992 (Fig. 2). Freshwater input showed greater variability from 1993 to 2000, with several years of above average freshwater input, including two extreme, positive deviations in 1993 and 1994. Negative deviations were also present during the latter period of the record, occurring in 1995, 1997, and 1999.

Salinity anomalies showed the opposite pattern from freshwater input, showing positive anomalies throughout the 1985–1992 period, with the exception of 1990 (Fig. 2). Salinity was lower than the long-term average in 1993 and 1994 and from 1996 to 1998. The 1996–1998 period salinity anomalies were not always opposite in sign from the freshwater input anomalies as one might expect. Positive salinity anomalies occurred in years of low freshwater input, in particular 1992, 1995, and 1999.

Spring water temperature showed the greatest variability of the physical variables, with cool and

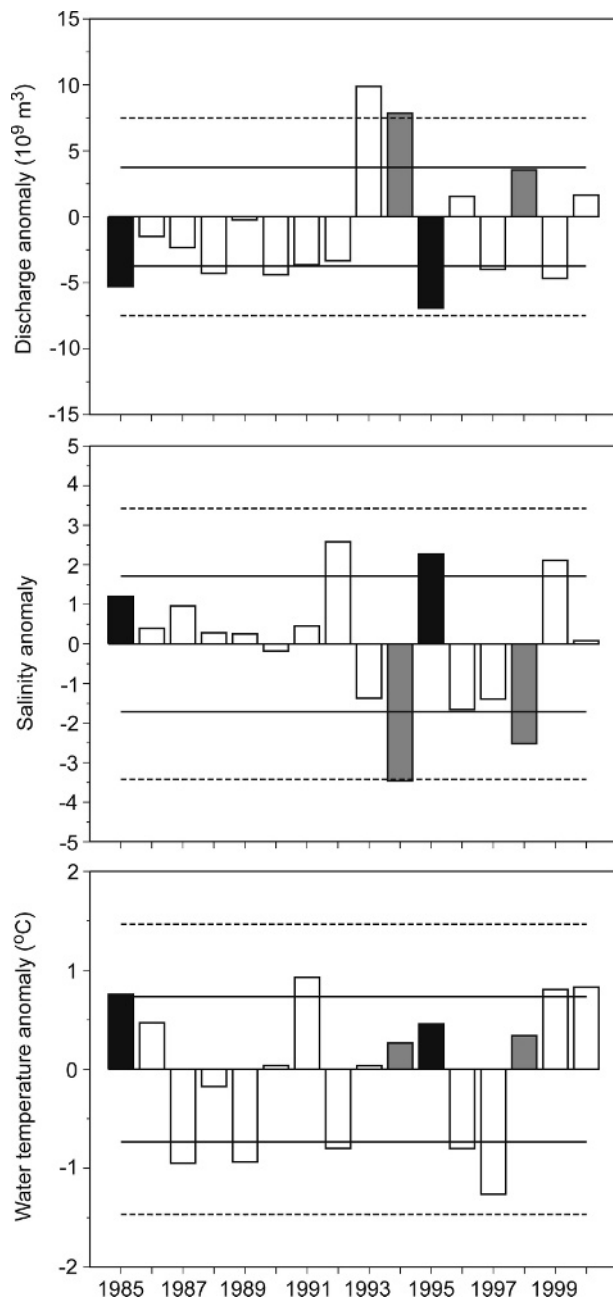


Fig. 2. Spring (March, April, and May) Susquehanna River discharge anomalies (top panel), spring salinity anomalies (middle panel), and spring temperature anomalies (bottom panel) for the upper Chesapeake Bay by year. Solid line represents ± 1 and the dashed line represents ± 2 standard deviations from the mean (0). Two characteristic dry years are represented by black bars and two characteristic wet years by gray bars.

warm periods present throughout the period of record (Fig. 2). Warm or cool temperatures did not appear to be associated with wet or dry conditions. The dry period of 1985–1992 had 3 warm springs (1985, 1986, and 1991) and 3 cool springs (1987,

1989, and 1992), indicating a disconnection between the magnitude of spring freshwater input and temperature.

The spatial extent of salinity was quite different between the selected dry (1985 and 1995) and wet (1994 and 1998) years (Fig. 3). During the dry years, the 15 isohaline was observed just south of 39°N in 1985 and around 39°N in 1995. The extent of the 15 isohaline during the wet years was approximately 38.5°N in 1994 and 1998. The result was a significant difference in the area of the upper Bay that contained low salinity water during wet and dry years. Residence times between wet and dry years were also quite different (Table 2), with the upper Bay flushing approximately half the time during the wet years (12–13 d) as in dry years (23–28 d).

BIOLOGICAL VARIABILITY

The dry years (1985 and 1995) were characterized by low abundance of *E. affinis* in the southern portion of the upper Bay (stations CB4.3C and CB5.2; Fig. 4). In 1985 there were low *E. affinis* abundances at all upper Bay stations; 1995 had moderate *E. affinis* abundances in the upper two stations. The wet year 1994 had high *E. affinis* abundance further down the Bay at stations CB3.3C, CB4.3C, and CB5.2. The wet year 1998 had the highest cumulative *E. affinis* abundance with a large peak at station CB3.3C. *A. tonsa* abundance was low during the same period and in 1994 showed an increasing trend at stations further south in the upper Bay.

Stepwise regression analysis revealed strong relationships between weather patterns and zooplankton abundance (Table 3). *A. tonsa* was correlated to weather patterns 6 and 9 at station CB3.3. Both weather patterns are associated with low precipitation (Table 1) and *A. tonsa* had higher abundances during the dry spring of 1995 (Fig. 4). No weather patterns were correlated with *A. tonsa* abundance at station CB4.3C and *A. tonsa* abundance at this station did not change in response to flow conditions. *E. affinis* was correlated to weather pattern 8 at stations CB3.3C and CB4.3C (Table 3). This weather pattern was rare during the winter (3.5% of total days) and was associated with warm, wet conditions (Table 1). During the wet spring of 1998, weather pattern 8 had a very high positive anomaly (Fig. 1). *E. affinis* was also negatively associated with weather pattern 3 and winter salinity at station CB4.3C (Table 2). Weather pattern 3 is the nor'easter pattern and is associated with wet and cold conditions (Table 1).

The residence times were different between dry (1985, 1995) and wet (1994, 1998) years (Table 2). Spring mean water temperature values between the

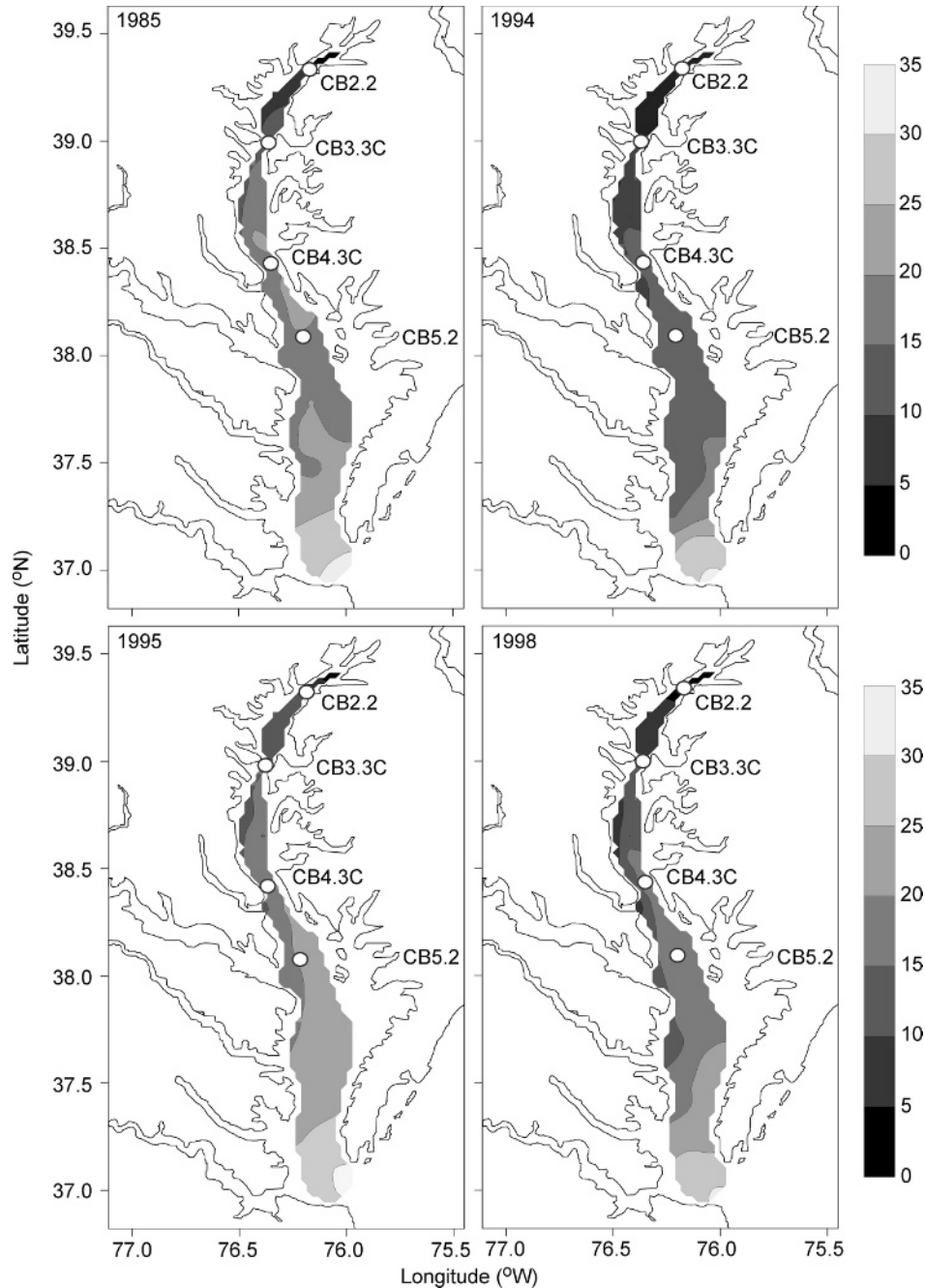


Fig. 3. Surface map of spring (mean of March, April, and May) Chesapeake Bay salinity during dry and wet years. Dry years are in the left column, wet years in the right. Location of Chesapeake Bay Program sampling stations are shown.

wet and dry years were similar, ranging from 16.0–16.5°C. These temperatures corresponded to a range of possible development times (egg to adult) for *A. tonsa* and *E. affinis*, 13–25 and 15–22 d, respectively (Table 2 and references therein). During the dry years, the maximum development times were similar to the residence time. During wet years, copepod development times were longer than the

estimated residence time of the upper Chesapeake Bay.

M. saxatilis juvenile index had negative anomalies throughout the 1985–1992 period followed by a period of positive anomalies and increased variability in 1993–2000 (Figs. 1 and 5). The wet years (1994 and 1998) that had high *E. affinis* abundance (Fig. 4) had positive anomalies for *M.*

TABLE 2. Residence time for the upper Chesapeake Bay ($>38.75^{\circ}\text{N}$), mean water temperature, and copepod development time (egg to adult) during dry and wet springs. *Acartia tonsa* development time from Heinle (1966), Zilloux and Wilson (1966), Heinle (1969), and Landry (1983) and *Eurytemora affinis* development time from Katona (1970), Hirche (1974), Heinle and Flemer (1975), and Poli and Castel (1983).

Year	Class	Residence Time (d)	Temperature ($^{\circ}\text{C}$)	<i>Acartia tonsa</i> (d)	<i>Eurytemora affinis</i> (d)
1985	Dry	22.7	16.5	13–25	15–22
1995	Dry	27.9	16.2	13–25	15–22
1994	Wet	12.3	16	13–25	15–22
1998	Wet	12.6	16.1	13–25	15–22

saxatilis (Fig. 5). The dry year 1985 had a negative anomaly, but the dry year 1995 had a small positive anomaly. The anomalies for the dry years were not as large in magnitude as the two wet years (1993 and 1996). *A. mitchilli* juvenile index showed an opposite pattern to that of *M. saxatilis*. Negative anomalies for *A. mitchilli* were observed since 1992 and greater variability during the earlier years of the data record. The wet years (1994 and 1998) both showed negative anomalies for *A. mitchilli* juvenile index.

Discussion

The weather patterns described by our analysis were similar to several other synoptic climatology studies performed in the mid-Atlantic region (Yarnal and Leathers 1988; Davis et al. 1993, 1997). The dominant weather pattern during the winter period was weather pattern 2, which corresponds to a continental high pressure system (Yarnal and Leathers 1988) that dominates the U.S. during winter. Davis et al. (1993) found that several different types of nor'easters occurred in the mid-Atlantic. Several low pressure weather patterns described in this study correspond to these nor'easter patterns (weather patterns 3 and 4). The corresponding surface conditions (temperature and precipitation) associated with each pattern also corresponded to the patterns described by Yarnal and Leathers (1988) for interannual and interdecadal variations in Pennsylvania climate. Yarnal and Leathers (1988) found two types of weather patterns, those usually associated with above normal temperatures and normal precipitation. These patterns correspond to our weather patterns 1, 4, 5, 8, and 9 (Table 1). The second group was characterized by below normal temperatures that can either be dry or wet depending on the location of the jet stream and storm track (Yarnal and Leathers 1988). These correspond to our patterns 2, 3, 6, 7, and 10.

Spring freshwater discharge from the Susquehanna River was correlated with winter weather

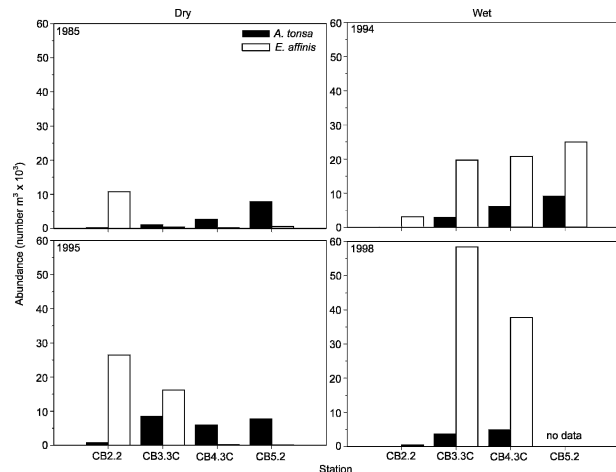


Fig. 4. Spring mean abundance of *Acartia tonsa* and *Eurytemora affinis* in characteristic dry and wet years for 4 stations in the upper Chesapeake Bay. Dry years are in the left column, wet years in the right. Error bars represent ± 1 standard deviation from the mean.

pattern frequencies (Miller et al. 2006). The discharge anomalies typically matched the salinity anomalies (Fig. 2), but some disconnect between these two variables did occur in the data record: e.g., 1996 was one of the wettest years on record due to the January blizzard of 1996 and subsequent high freshwater input that occurred throughout the year (Kimmel and Roman 2004; Roman et al. 2005). The year 1996 was also very cold, having a large, negative water temperature anomaly. This delayed the discharge into the Bay until later in the year as water was stored in the basin in the form of snow (Najjar 1999). Further evidence of the effect of 1996 was the negative discharge anomaly in 1997 having no effect on the spring salinity in 1997, which had a negative anomaly for the same period. Spring water temperature showed greater variability during the data record and was often unrelated to discharge anomalies. Using 1996 as an example, the year-long cold temperatures may have had an effect on the following spring (1997) temperature, which showed a large negative anomaly. The series of wet-dry cycles that we observed, particularly during the 1993–2000 period, mirror the paleorecord. Cronin et al. (2000) found 14 wet-dry cycles in the Chesapeake Bay over the last 500 yr and as a result, the salinity in the mesohaline portion of the Bay often varied by a factor of 2. This variability was shown in the change in spatial extent of low salinity water observed in wet and dry years (Fig. 3).

Winter climate affected spring *E. affinis* abundance to a greater extent than *A. tonsa*. Winters with warm, wet conditions favored high discharge into the upper Bay and resulted in elevated abundance of *E. affinis* and more *E. affinis* further down estuary

TABLE 3. Coefficients of determination (r^2), adjusted r^2 , p values, and positive and negative correlate variables for a stepwise regression of species abundance and winter climate pattern frequency (WP), winter salinity, and winter temperature.

Species	Station	r^2	Adjusted r^2	p Value	Positive Correlate	Negative Correlate
<i>Acartia tonsa</i>	CB2.2	0.47	0.39	0.02	WP 7	
					WP 9	
<i>Acartia tonsa</i>	CB3.3C	0.40	0.31	0.03	WP 6	
					WP 9	
<i>Acartia tonsa</i>	CB4.3C					
<i>Eurytemora affinis</i>	CB2.2	0.51	0.44	0.009	WP 7	
					WP 9	
<i>Eurytemora affinis</i>	CB3.3C	0.34	0.29	0.02	WP 8	
<i>Eurytemora affinis</i>	CB4.3C	0.69	0.61	0.002	WP 8	WP 3
						Salinity

(Fig. 4, Table 3). These results agree with our previous work that found that elevated abundances of *E. affinis* were associated with high freshwater input and associated changes in hydrologic conditions, such as salinity and temperature (Kimmel and

Roman 2004). Increased discharge also results in high detritus input, a potential food source for *E. affinis* since it may be consumed directly (Heinle and Flemer 1975; Heinle et al. 1977) or serve as a substrate for particle attached bacteria that *E. affinis* consume (Crump et al. 1998). Wet periods also alter the location of the estuarine turbidity maximum (through increased discharge), an important nursery area for anadromous fish in the upper Chesapeake Bay (North and Houde 2001, 2003) and a region of high *E. affinis* abundance, presumably due to a trapping mechanism (Castel and Veiga 1990; Roman et al. 2001). *E. affinis* was negatively correlated to weather pattern 3 at station CB4.3C (Table 3). This was surprising because weather pattern 3 was associated with high precipitation and cool temperatures (Table 1).

A. tonsa abundance in spring was not as strongly related to winter climate as *E. affinis*. Though the stepwise regression suggested relationships between *A. tonsa* and winter weather pattern variability, the relationships were not as consistent as *E. affinis* (Table 3) and did not result in large changes in abundance (Fig. 4). Several reasons may explain why *A. tonsa* is less responsive to climate forcing. It is possible that other factors, such as top-down control by predators (Dippner et al. 2001) or food limitation are more important, though the work of White and Roman (1992) suggest food limitation does not control *A. tonsa* egg production during summer. Food limitation may be important in wet springs as turbid conditions in the upper Bay prevent large blooms of phytoplankton, which typically occur farther south (Harding 1994). *A. tonsa* requires near continual feeding and high ambient phytoplankton abundance to support its high rate of reproduction (Paffenhöfer and Stearns 1988).

The two copepod species had a similar relationship to cool-dry weather at the northernmost station (CB2.2; Fig. 4, Table 3). Each species responded to drier winter weather and the resultant lower

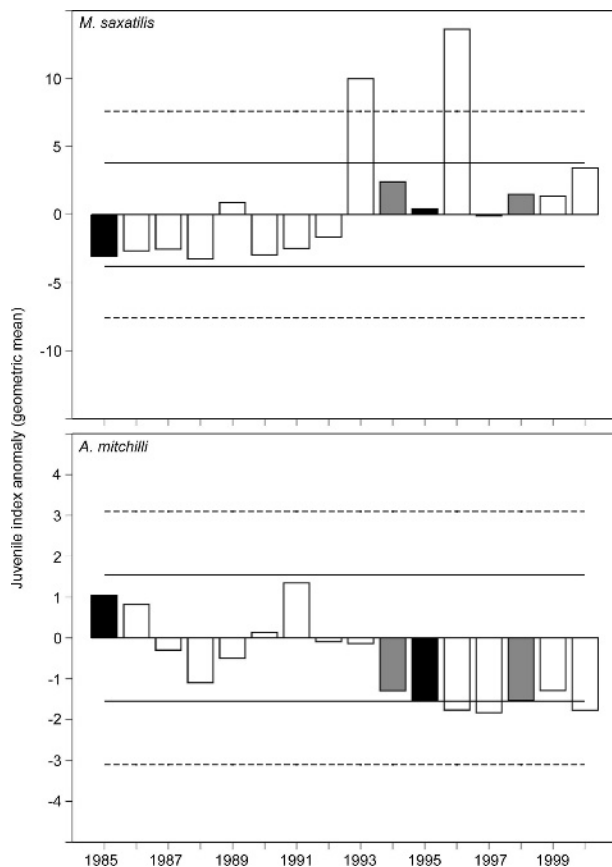


Fig. 5. Annual juvenile index anomalies for *Morone saxatilis* (striped bass) and *M. americana* (white perch). Solid line represents ± 1 and the dashed line represents ± 2 standard deviations from the mean (0). Two characteristic dry years are represented by black bars and two characteristic wet years by gray bars.

discharge at station CB2.2. This may be related to the low salinity conditions found at this station during high flow. *A. tonsa* is considered to be euryhaline and is capable of surviving at near freshwater conditions (Cervetto et al. 1999); Bradley (1991) suggests that lower temperatures and lower salinities tend to favor *E. affinis* over *A. tonsa* in Chesapeake Bay. *E. affinis* is also considered euryhaline and is more readily adaptable to lower salinity conditions (Lee 1999); this species experiences a negative effect on nauplii survival at extremely low salinities (Devreker et al. 2004).

The residence time may also be a factor affecting the response of each copepod species to winter weather conditions (Table 2). The development time for both copepod species was similar as development time is strongly related to temperature (Table 2 and references therein). Both of the highlighted wet and dry years had similar temperatures. During dry years, it is possible for *A. tonsa* and *E. affinis* to develop from egg to adult without being flushed from the upper Bay region. This is especially critical for *A. tonsa*, a broadcast spawner whose eggs are susceptible to advective transport. *E. affinis* females carry their eggs and this, along with reduced salinities and a tendency to remain near the bottom, may explain why *E. affinis* abundance is restricted to the upper Bay. During wet years the residence time for the upper Bay is approximately 50% less than dry years. There is greater potential for the flushing of *A. tonsa* eggs from the upper Bay resulting in higher abundance further down the estuary during wet years. Note that Fig. 4 does not show a major difference in the abundance of *A. tonsa* between wet and dry years. This suggests that other factors are likely controlling *A. tonsa* abundance, such as gelatinous zooplankton predation as suggested by zooplankton size spectra (Kimmel et al. 2006). *E. affinis*, on the other hand, is a brooding copepod and is able to maintain its position in upper Bay (station CB3.3C) more readily than *A. tonsa*, a broadcast spawner. *E. affinis* was also found further down estuary during wet periods suggesting some flushing of *E. affinis* eggs during wet years (Fig. 4).

The response of *E. affinis* to weather patterns suggests that high abundances of *E. affinis* in spring may be predictable events. These spring copepod blooms play a critical role in the recruitment success of anadromous fish such as *M. saxatilis* and *M. americana* (white perch), both of which spawn in the upper Chesapeake Bay. *E. affinis* is an important food resource for larval striped bass (Uphoff 1989; North and Houde 2003). Both fish juvenile indices show positive anomalies during years with above average discharge (Figs. 1 and 5). Spring abundances of *E. affinis* were positively correlated to the

M. saxatilis juvenile index (Spearman's $\rho = 0.65$, $p < 0.05$) and negatively correlated to the *A. mitchilli* juvenile index (Spearman's $\rho = -0.57$, $p < 0.05$). While the link appears strong between spring *E. affinis* abundance and anadromous fish, the strongest years for juvenile fish indices are not related to the highest spring zooplankton abundances. There are several possible explanations for this lack of coherence. Secor and Houde (1995) found that *M. saxatilis* cohorts that experience average temperature (15–20°C) had lower mortality rates than those experiencing higher or lower temperatures. Secor and Houde (1995) also found that observed zooplankton densities did not affect growth rates of *M. saxatilis*. Habitat characteristics for anadromous fish may be more critical to producing successful year classes than zooplankton food resources. Recent work by Kraus and Secor (2005) found that for dominant year classes of *M. americana* (a congener of striped bass), brackish water habitat was most important; for all other year classes, freshwater habitat was more important. The juvenile index survey is a yearly mean compiled from three samplings taken during July, August, and September, incorporating conditions beyond the spring spawning period. This may explain the very wet years 1993 and 1996 having the highest juvenile indices since wet, cool conditions persisted into summer (Fig. 5). Fish juveniles are also affected by other conditions, such as the spawning stock biomass, predation, density-dependent effects, and environmental conditions that extend beyond spring.

The relationship between zooplankton dynamics and weather pattern frequencies suggests that we should be able to predict the response of *E. affinis* and *A. tonsa* to climate change. Potential effects of climate change for the mid-Atlantic region of the U.S. have been explored (Najjar et al. 2000). Since 1895, the mid-Atlantic region has become wetter (+10%) and warmer (+0.5°C; Polsky et al. 2000). Climate models suggest the trend is likely to continue with a 32% increase in spring and summer rainfall over the Susquehanna River basin (Crane and Hewitson 1998) and an increase in annual stream flow of $24 \pm 13\%$ by the year 2095 (Najjar 1999). This prediction may be a reflection of the recent wet-dry climate cycles seen in the Chesapeake Bay region (Cronin et al. 2000). Based on our analysis of zooplankton composition and freshwater discharge into Chesapeake Bay under different climate conditions we have formulated a conceptual model of spring zooplankton distribution for wet and dry periods (Fig. 6). This conceptual model is based on the response of each species to winter climate. A winter consisting of weather patterns exhibiting above average temperatures and low

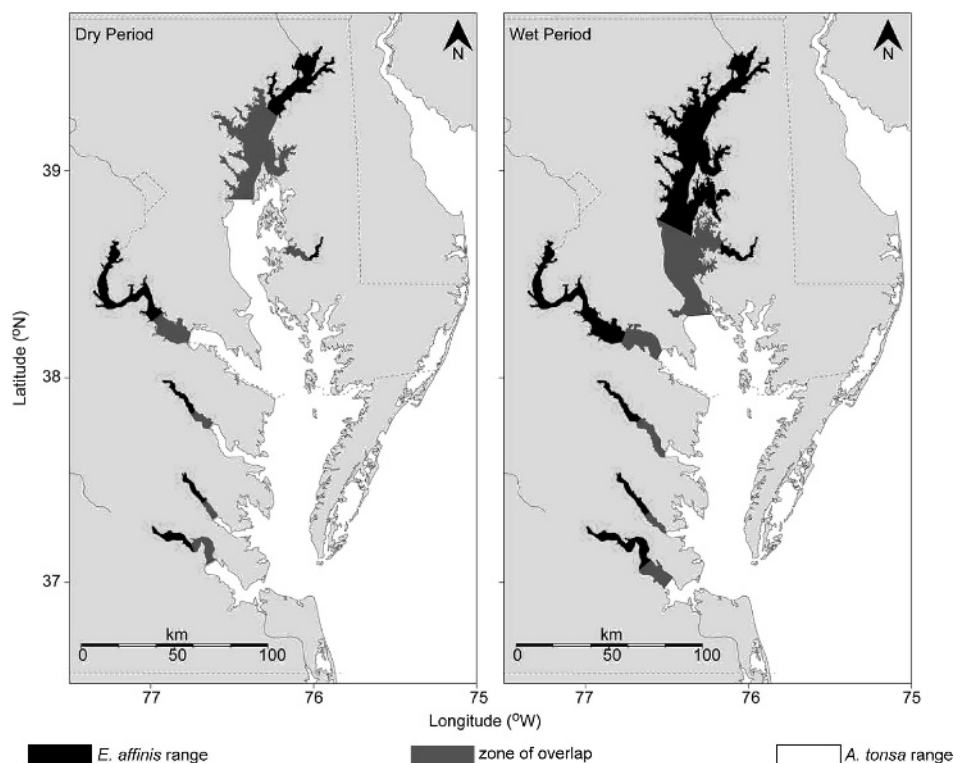


Fig. 6. Conceptual diagram of the spring geographical distribution of *Acartia tonsa* and *Eurytemora affinis* in the Chesapeake Bay during a dry period and a wet period.

precipitation will result in the decrease in the range of *E. affinis* and an increase in the range of *A. tonsa* in Chesapeake Bay during spring. A winter consisting of weather patterns resulting in high precipitation and high spring discharge will result in an increase in the range of *E. affinis* and a decrease in the range of *A. tonsa* in Chesapeake Bay during spring. We conclude that synoptic climatology of winter weather patterns is a useful tool to formulate short-term forecasts (3–6 mo) of spring zooplankton composition and abundance in the upper portion of Chesapeake Bay.

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